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GENITALIC RECASTING OF *POANES* AND *PARATRYTONE* (HESPERIIDAE)

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ABSTRACT. Hesperiine skipper genera in stable use in the United States and Canada at least since 1955 are gaining "authority through repetition." But critical comparison of genitalia shows that many of those genera are grossly misdefined and polyphyletic. Problems usually extend into the neotropics. On the basis of male and female genitalic characters (and about 200 KOH-treated dissections), I precisely redefine both *Paratrytone* Godman, which is high montane in much of the central and southern Rocky Mountains of the U.S. but especially in Mexico, and a compact group comprising the "terrestrial species" of *Poanes* Scudder (as opposed to the "marsh dwellers"), which range from southern eastern and central Canada, and from California and the central Rocky Mountain region of the U.S., to northern South America (Colombia, Venezuela, and Ecuador). Two-thirds (eight) of the species currently in *Paratrytone* (including *melane* [Edwards]) go elsewhere—mostly to *Poanes*; but *Paratrytone* gets *snowi* (Edwards) from *Ochlodes* Scudder. *Poanes* also gets *macneilli* **new species** from the Sierra Nevada de Santa Marta in northern Colombia but loses two Mexican and Central American species. The fuller treatment given *Poanes* includes capsule geographic distributions of its species and discussion of male genitalia at the specific level. *Poanes zabulon* (Boisduval & Le Conte) and *Poanes taxiles* (Edwards) are unquestionably distinct species. **New combinations:** *Poanes niveolimbus* (Mabille), *Poanes monticola* (Godman), *Poanes capta* (Miller & Miller), *Poanes ulphila* (Plötz); *Paratrytone snowi* (Edwards); *Ochlodes batesi* (Bell). **New synonymies:** *Poanes taxiles* (Edwards) = *P. psaumis* (Godman); *Poanes monticola* (Godman) = *P. capta* (Miller & Miller). **Incertae sedis** (temporary floaters): *rolla* (Mabille) and *benito* Freeman ex *Poanes*; *argentea* (Weeks) and *barroni* Evans ex *Paratrytone*.

Additional key words: genitalia (male and female), taxonomy, nearctic, neotropical, *Ochlodes*.

Our butterflies are supposed to be taxonomically well-known. Consider our skippers: half the nearly 300 species recorded from the United States are hesperiines, and their generic placement has not changed since the American hesperiine volume of Evans (1955). With the flood of North American butterfly books and checklists in recent decades, these stable skipper genera are gaining what I call "authority through repetition." In fact, much is generically wrong.

If critically studied and compared, genitalia are as valuable for group-

ing related species in higher categories like genera as they are for distinguishing species. Over the past six years, I have been genitalically reviewing (in both sexes) much of the nearctic hesperiine fauna—and some of its neotropical connections—with an eye to better defining our "familiar" genera.

Major errors reported so far—involving *Atalopedes* and *Hesperia* (Burns 1987, 1989), *Amblyscirtes* and some of its relatives (Burns 1990), and *Atrytone* and *Mellana* (Burns unpubl.)—are the tip of a taxonomic iceberg. There are so many hidden mistakes that I need a faster way of addressing them. Some quick remedies will, of necessity, be partial or transitional. But dispatch is desirable because faulty classification continues to distort information in our new butterfly books, making broader biological generalizations and comparisons meaningless.

This paper is an effort to recast *Poanes* and *Paratrytone*—two sizable polyphyletic genera that include nearctic species—without going into needless detail. Since the primary problem at this stage is bringing related species together while dismissing the rest, problems at and around the species level (which have always intrigued me), and analyses of phylogeny, get short shrift. Traditional butterfly characters of wing color and pattern are dispensable, owing especially to rampant parallelism and convergence; but characters of the genitalia are crucial. I am resurrecting eleven genitalic illustrations from the turn of the century and the mid-twenties both to acknowledge pioneer workers whose forgotten figures still convey what we need to know (Godman 1900, Skinner & Williams 1924a, 1924b) and to save time (new and better genitalic figures would be long in coming).

A PART FROM *POANES* SCUDDER

I am actually concerned here with a subgroup of what now passes as *Poanes*, to wit, the "ordinary terrestrial species" such as *hobomok* (Harris), *zabulon* (Boisduval & Le Conte), and *taxiles* (Edwards), as opposed to the four specialized "marsh dwellers," *massasoit* (Scudder), *viator* (Edwards), *aaroni* (Skinner), and *yehl* (Skinner). Though all are related, I cannot yet say whether the peculiar *massasoit*—the type species of *Poanes*—is truly congeneric with the terrestrial species (or even, for that matter, with the other marsh dwellers). My continued application of the generic name *Poanes* to the terrestrial species is conservative and provisional.

With flamboyant asymmetric titillators augmenting the penis of the male and correspondingly and indescribably elaborate wrinkles complicating the copulatory duct of the female, the genitalia in the terrestrial species of *Poanes* are collectively odd; but, at the same time,

they are interspecifically similar. In other words, the species are minor variations on a major theme.

In defining this theme—this genitalically compact group—I have extracted shared critical features from a total of 75 KOH-treated genitalic dissections (45 males, 30 females) of all included species. My working description of each sex has been read against each of the individual dissections in order to polish it and to better accommodate variation.

Many additional genitalia have been examined and compared in connection with the grander setting, which involves (among other things) the marsh dwellers, some Asian kin, and certain skippers now in *Poanes* that cannot possibly belong. Specifically, *rolla* (Mabille) from Costa Rica and Panama and the much more recently described *benito* Freeman from southern Mexico superficially resemble *Poanes* without being anywhere near it. Together, they are going to another genus (Burns unpubl.).

The terrestrial species of *Poanes* range from southern eastern and central Canada, and from California and the central Rocky Mountain region of the United States, to northern South America (Colombia, Venezuela, and Ecuador).

Male Genitalia
(Figs. 1–16)

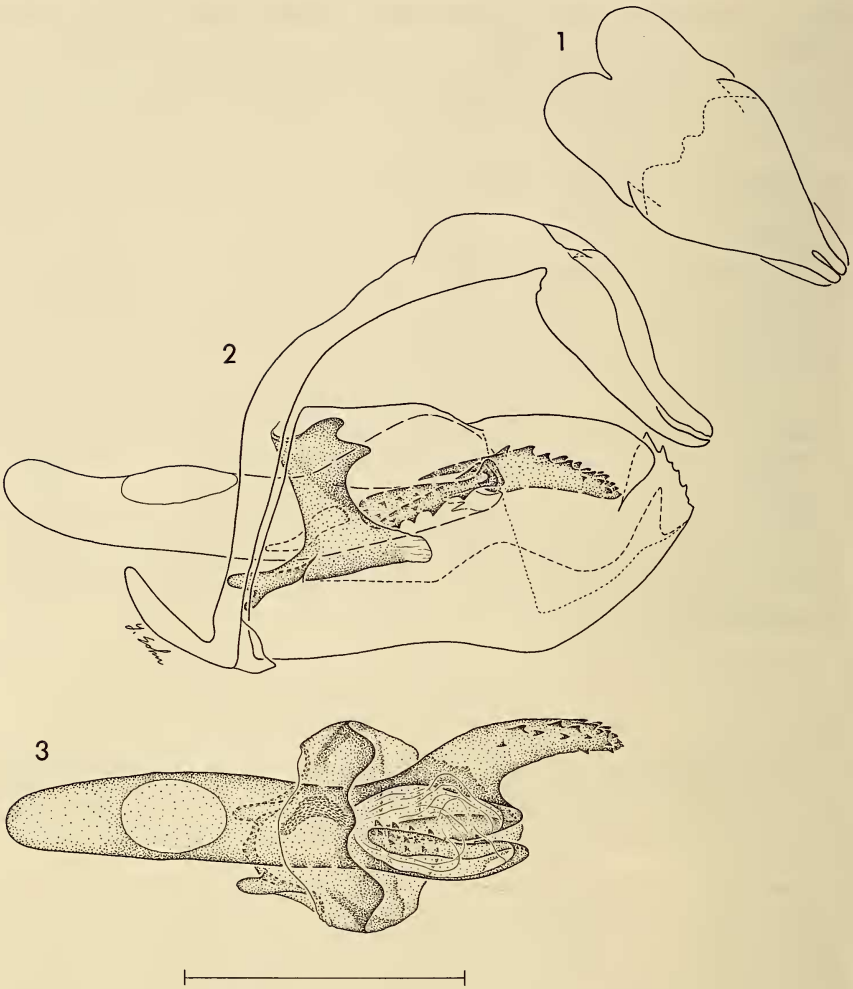
The valva in lateral view is longer than high and basically rectangular, but its posterior end is curved rather than straight. *This curved distal end is* set off dorsally from the body of the valva by a vertical slit or notch and is itself *divided into two dorsally-pointing projections, one more lateral (and always dentate), the other more medial* (Figs. 2, 5, 6, 8–16).

Three long, distinctive, asymmetric titillators sprout from the distal end of the aedeagus—one on the right, one toward the middle, and one on the left. Both *the right and left ones are* conspicuous and *conspicuously dentate* (Figs. 2, 3, 5–16). *The right titillator, which is heavy and rigid, always extends backward* (also, in many cases, downward), well beyond the body of the aedeagus. Although the central titillator shares an origin with the right one (Figs. 3, 6, 7), it approaches the left one; and, together, *the central and the left titillators, which are much more delicate than the right, fold on themselves 180° to run forward inside the aedeagus* (see especially Fig. 3) when it is at rest (i.e., when the vesica is not everted).

The aedeagus is encircled by a massive sclerotized ring, the anellus, which is medial to the vinculum and the anterior ends of the valvae. Wide all the way around, the anellus becomes extra wide ventrally (where it incorporates the juxta). Anteroventrally it extends forward beneath the aedeagus, finally forming a pair of short anterior projections (see especially Figs. 2, 3, 5, 7, but also 8–10, 12).

In lateral view *the long,* more or less *narrow gnathos lies close under the uncus* (Figs. 2, 5, 8–11, 14–16). In dorsal view the uncus suggests a caudally-tapering triangle, but the immediately anterior tegumen fails to prolong the triangular effect (Figs. 1, 4). Distally the uncus splits into paired prongs (interspecifically variable in length) which are in contact or close (Figs. 1, 4).

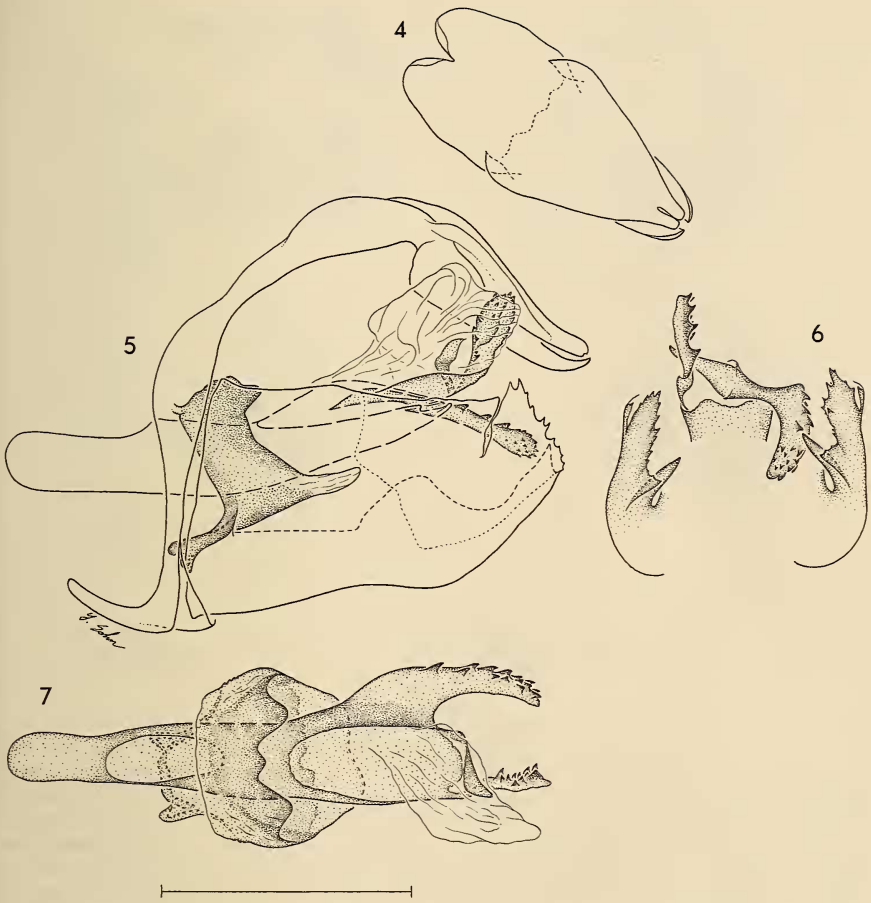
The saccus is short (Figs. 2, 5, 8–16).



FIGS. 1–3. Male genitalia of *Poanes macneilli*, holotype, from east above San Pedro de la Sierra, Sierra Nevada de Santa Marta, 2900–3900 m, COLOMBIA, 7 March 1975, M. J. Adams (genitalic dissection no. X-2352) (USNM). Scale = 1.0 mm. **1,** Tegumen, uncus, and gnathos in dorsal view; **2,** Complete genitalia (minus right valva) in left lateral view, with anellus and all three titillators stippled and cornutus outlined by dashes (anterior to titillators and medial to anellus); **3,** Aedeagus and anellus in dorsal view, with central and left titillators in resting position (folded 180°) and the scouring-pad cornutus showing within the aedeagus (under the top of the anellus).

Female Genitalia
(Figs. 17, 18)

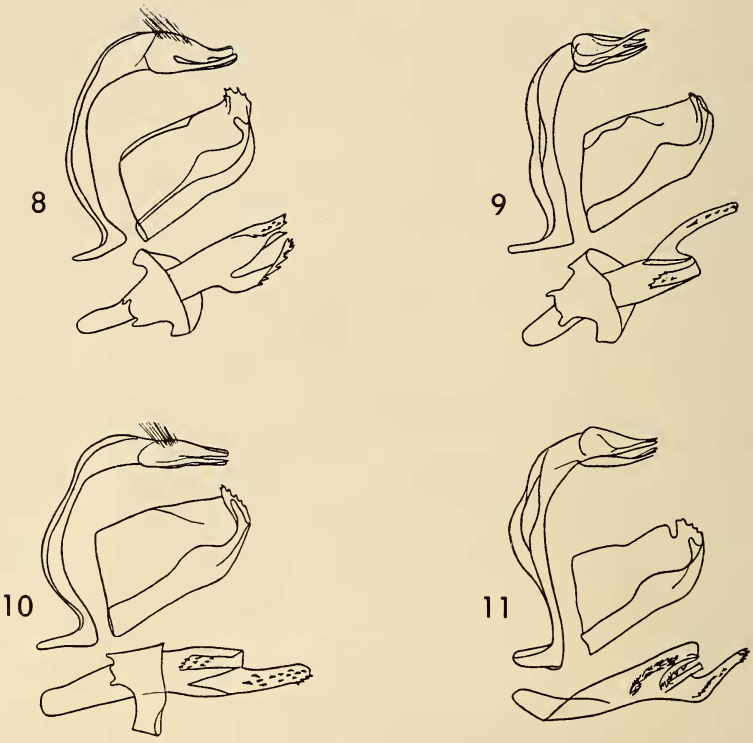
The short, broad ductus bursae initially runs forward but then bends upward (Fig. 18) and to the left (Fig. 17), as well. It is membranous, and usually somewhat longitudinally



FIGS. 4–7. Male genitalia of *Poanes azin* from Bogotá, COLOMBIA, 4 April 1920, F. Clark (X-2965) (USNM). Vesica everted to unfold the flexible central and left titillators, which project from the end of the aedeagus. Scale = 1.0 mm. **4,** Tegumen, uncus, and gnathos in dorsal view; **5,** Complete genitalia (minus right valva) in left lateral view, with anellus and all three titillators stippled; **6,** Distal ends of valvae (showing the outer [dentate], and inner, dorsally-pointing projections on each valva) and aedeagus (showing all three titillators) in posterior view; **7,** Aedeagus and anellus in dorsal view, with central and left titillators unfolded.

wrinkled, both ventrally and dorsally; but it is sclerotized, and transversely wrinkled-and-grooved, laterally. The heavy, conspicuous wrinkles-and-grooves are extremely intricate and not altogether transverse. The ductus bursae does show some ventral sclerotization where it bends upward and some dorsal sclerotization at its origin. There, just above and behind the ostium bursae, a caudally convex shelf—variably sclerotized, and often at least centrally membranous—curves across the midline.

Large, paired, rounded, variably sclerotized and internally spinulose pouches lie just above, behind, and to the sides of the ostium bursae and this arched shelf. After giving



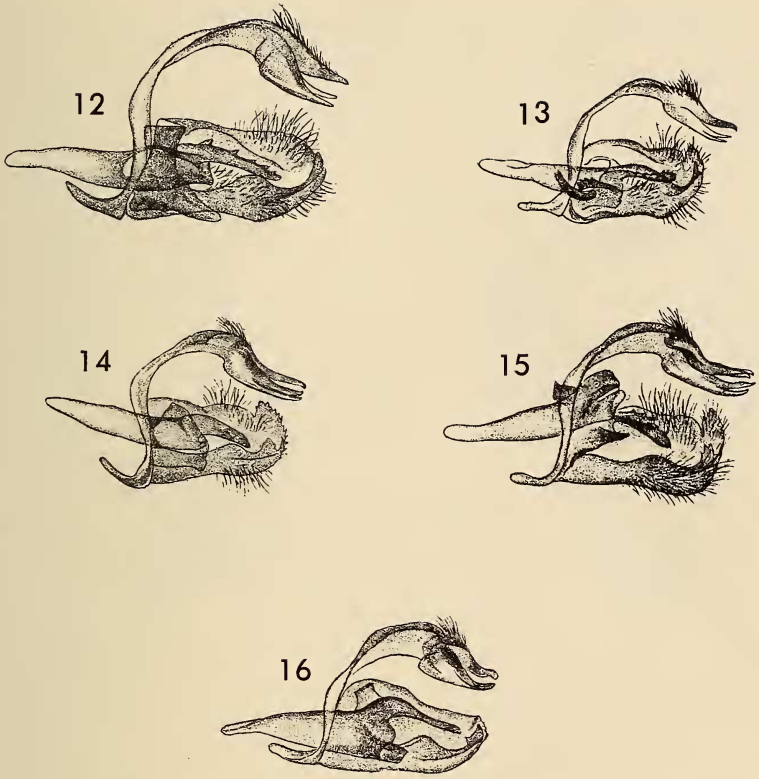
FIGS. 8–11. Male genitalia of four species of *Poanes* ex Skinner and Williams (1924a). All ×15. Drawn from slide mounts in which *parts are not perfectly oriented,* these exploded figures show (top to bottom) tegumen, uncus, gnathos, vinculum, and saccus in left lateral view; the right valva in medial view (good for seeing the inner, and dentate outer, dorsally-pointing projections); and the aedeagus and anellus in variable views (the anellus, in more or less ventral view when shown, has sometimes rotated relative to the aedeagus; the large, rigid titillator extending backward is always the right one, no matter where it appears). **8,** *Poanes hobomok* from Avon, Connecticut, U.S.A.; **9,** *Poanes zabulon* from Havre de Grace, Maryland, U.S.A.; **10,** *Poanes taxiles* from Chimney Gulch, Colorado, U.S.A.; **11,** *Poanes melane* from southern California, U.S.A. (this figure omits the anellus but shows all three titillators, as well as *melane*'s scouring-pad cornutus which most *Poanes* lack).

rise to the apophyses anteriores, the eighth tergite continues downward to fuse broadly with the dorsal side of each pouch.

From the innermost ends of these pouches, finely spinulose bands extend backward (Fig. 17), diverging through a membranous to very lightly spinulose area, to reach the outer edges of a thick, well-sclerotized, spinulose to centrally bristled transverse element (just in front of the ovipositor lobes), which is variously shaped, particularly along its posterior margin. It usually projects ventrad.

PARATRYTONE GODMAN

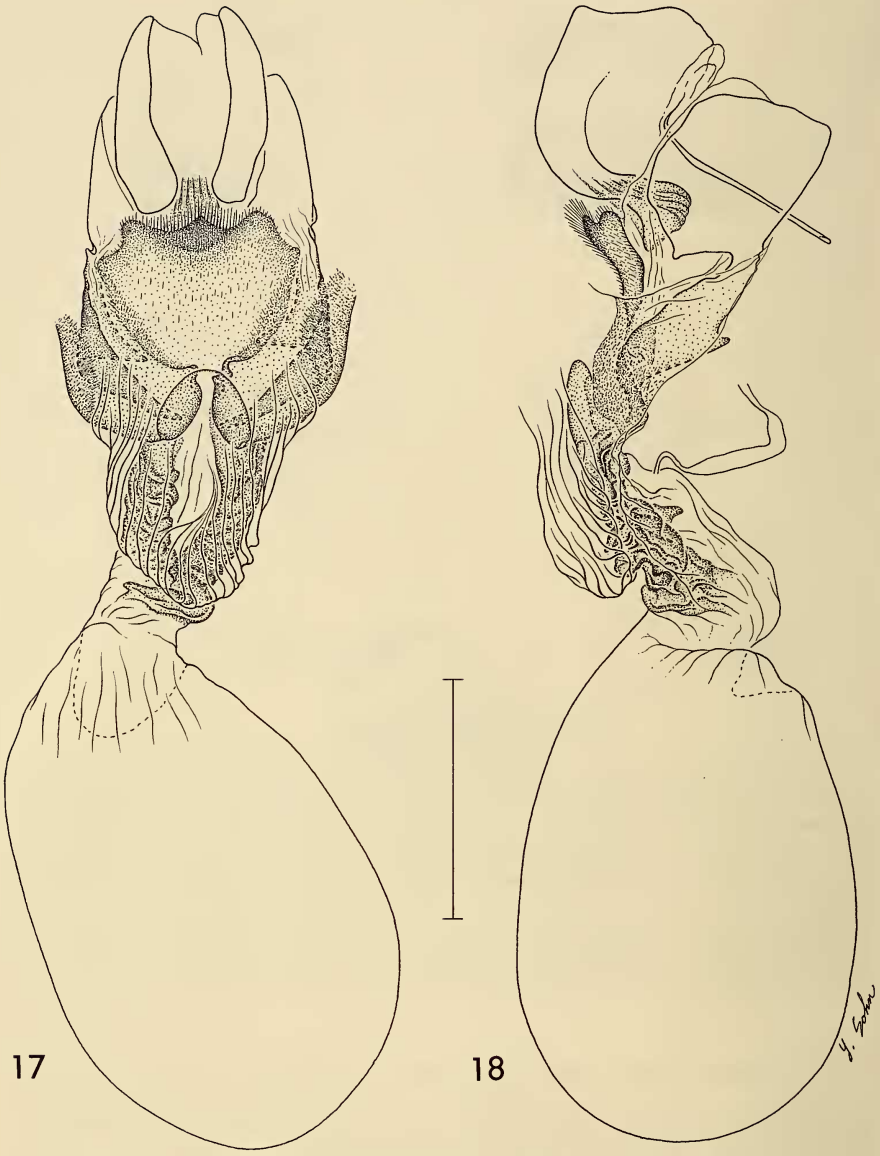
Paratrytone is a highly distinct genus that is related to the terrestrial species of *Poanes.* (However, those species of *Poanes* are much closer



FIGS. 12–16. Male genitalia of five species of *Poanes* ex Godman (1900: plate 94), who treated them all as *Atrytone*. Drawn from slide mounts in which *parts are not perfectly oriented*, these figures show complete genitalia (minus left valva) in left lateral view. Like the Skinner and Williams figures, they present the inner surface of the right valva, whereas mine present the outer surface of the left valva. **12,** *Poanes zabulon* (the gnathos has artificially sagged too far below the uncus); **13,** *Poanes melane* (again, the gnathos has sagged a bit, but *melane*'s scouring-pad cornutus, which most *Poanes* lack, appears as a dark arc behind the bottom of the vinculum); **14,** *Poanes monticola*; **15,** *Poanes niveolimbus*; **16,** *Poanes inimica*.

to *Ochlodes* than they are to *Paratrytone*—so much so, in fact, that at least terrestrial *Poanes* and *Ochlodes* may ultimately merge.) Males of *Paratrytone* (but also of *Ochlodes*!) have a large stigma on the dorsal surface of the forewing, whereas males of the terrestrial species of *Poanes* do not.

Though I am concerned with all of *Paratrytone*, instead of a subgroup of it, I am drastically changing its composition: six of the nine species included by Evans (1955) must go—four of them to *Poanes*, along with yet another species more recently described and likewise misplaced in *Paratrytone* (see Notes on the Terrestrial Species of *Poanes* below).



FIGS. 17, 18. Female genitalia of *Poanes macneilli* from north of San Sebastian, Sierra Nevada de Santa Marta, 2800–3400 m, COLOMBIA, 15 February 1975, M. J. Adams (X-2365) (collection of C. D. MacNeill). Scale = 1.0 mm. **17,** Ovipositor lobes, eighth tergite with apophyses anteriores, sterigma, and bursa copulatrix in ventral view; **18,** The same, plus the right apophysis posterioris and part of the ductus seminalis, in right lateral view.

The other two species that Evans wrongly stuck in *Paratrytone*—*argentea* (Weeks) from Bolivia and *barroni* Evans from Ecuador—are temporarily without a proper home. (I am setting them in *incertae sedis*, like *simius* Edwards, formerly of *Amblyscirtes* [Burns 1990].) Early in this study I concluded, from Weeks's (1905: plate 15, fig. 2) color paintings of *argentea*, its Bolivian provenance, and its unavailability to Evans (1955:350), that *argentea* did not fit in *Paratrytone*; and eventual dissection of its male genitalia bore me out totally. Evans (1955:351) described *barroni* (in the company of other species that do not really belong in *Paratrytone*) in great superficial detail from a single female from 915–1220 m in Ecuador. I have not gone after this type because neither her looks nor her low latitude and low altitude relate to true *Paratrytone*. Correctly defined and flushed of misfits, *Paratrytone* displays a tidy, restricted geographic distribution that makes biologic sense (see below).

I am also removing the montane Hispaniolan species *batesi* (Bell) which went from *Poanes*, where it was originally described (Bell 1935), to *Choranthus* (Evans 1955), where it had absolutely no business, to *Paratrytone* (Miller 1966), where it has remained (Riley 1975, Schwartz 1989). Even though Miller (1966) examined and compared male and female genitalia of representative species of *Poanes* and *Paratrytone* together with those of all of Evans's species of *Choranthus*, he erred in his placement of *batesi*. Bell (1935) came close to the mark in putting *batesi* in *Poanes*—but not in specifically relating it to *yehl*, *rhexenor* Godman, *polyclea* Godman, and *aphractoia* Dyar. These last three species, all Mexican, are the only ones of the nine that Evans (1955) had in *Paratrytone* that really belong there. (It is worth noting that *Paratrytone* Godman 1900, with *rhexenor* as type, should not be confused with its homonym *Paratrytone* Dyar 1905, which, with *howardi* Skinner [=the marsh dweller *aaroni*] as type, is a synonym of *Poanes*.) Having compared KOH-treated genitalic dissections of two pairs of *batesi* with those of *Paratrytone*, *Poanes*, and a dozen species of *Ochlodes* (both sexes, 33 dissections), I propose the **new combination** *Ochlodes batesi*. As stated above, *Ochlodes* and *Poanes* may prove too close for bigeneric comfort. For now it is obvious that the genitalia of *O. batesi*, while different from those of the terrestrial species of *Poanes*, are ever so much nearer to them and especially to those of some species of *Ochlodes* than they are to those of *Paratrytone*.

As if in compensation for the near-total purge, *Paratrytone* gets *snowi* (Edwards) (**new combination**) from *Ochlodes* plus some undescribed, high-altitude Mexican species (Burns & MacNeill unpubl.). It also keeps *decepta*, one of two species described in *Paratrytone* by Miller and Miller (1972)—but it loses the other one, which belongs with the ter-

restrial species of *Poanes* (see below): figures of the male genitalia (Miller & Miller 1972:figs. 17, 18), despite poor representation of the diagnostic aedeagi, unmistakably show one species in each genus.

To summarize, *Paratrytone* recast contains *rhexenor*, *snowi*, *decepta*, *polyclea*, *aphractoia*, and some undescribed species (one of which, however, is probably *pilza* Evans [1955:343] described as a subspecies of *snowi* from southern Mexico ["Pinal, Puebla, 8000 feet"]).

In *Paratrytone*, as in the terrestrial species of *Poanes*, the genitalia in each sex are clearly variations on a single singular theme. The most salient traits are, in males, two symmetric pairs of aedeagal titillators (one dorsal, one ventral) along with a basally massive gnathos and, in females, a ventrally projecting structure at the back of the lamella postvaginalis (hence distally located, just in front of the ovipositor lobes) that suggests human lips.

In characterizing *Paratrytone* I have studied and compared a total of 86 KOH-treated genitalic dissections (47 males, 39 females). Again, I have honed my working description of each sex while hearing it read aloud as I slowly reexamined each dissection.

Far more limited in geographic and altitudinal distribution than the terrestrial species of *Poanes*, *Paratrytone* is high montane (ca. 2000–3100 m), mostly in Mexico but also in much of the central and southern Rocky Mountains of the United States (extreme southeastern Wyoming, Colorado, New Mexico, and Arizona).

Male Genitalia
(Figs. 19–23)

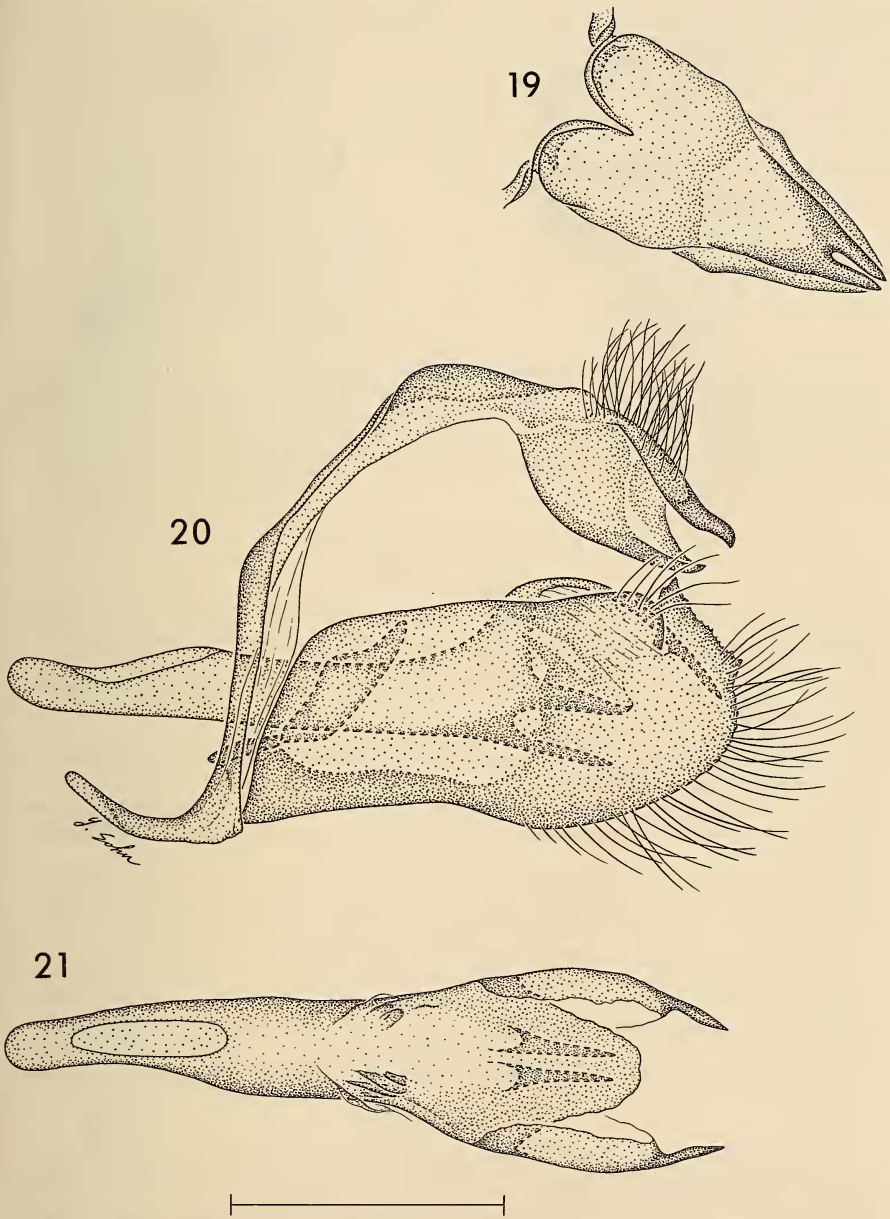
Much as in *Poanes*, the valva in lateral view is roughly rectangular, but its posterior end is sometimes more angled (Fig. 23) than rounded. Again as in *Poanes*, the distal end is set off dorsally from the body of the valva by a vertical slit or notch; but *this end is made up of only one dorsally-pointing projection (which may or may not be dentate)* (Figs. 20, 22, 23). Because *there is no second dorsally-pointing projection arising from its inner surface*, the distal end of the valva is much simpler than it is in *Poanes*.

Two pairs of symmetric titillators spring from the distal end of the aedeagus—one dorsally, one ventrally. All four titillators extend backward (they may also go upward or downward) *and all lack teeth, but each ends in a single delicate point* (Figs. 20–23). (The titillators vary greatly in length, the ventral pair vanishing in at least one species [*Paratrytone aphractoia*].)

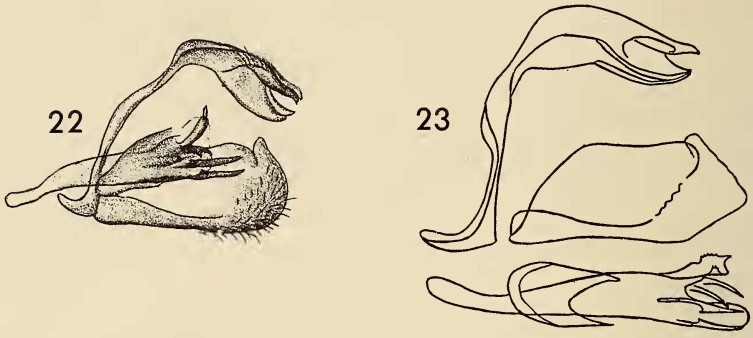
A simple juxta lies ventral and lateral to the aedeagus (Figs. 20, 23), medial to the vinculum and the anterior ends of the valvae. *It is basically* U*-shaped* (in dorsal or ventral view) with its central, transverse, more or less straight-edged base midventral and its two arms extending backward. Each arm has a single twist, and the arms usually bend dorsally (Fig. 20) but sometimes run straight back.

In lateral view *the gnathos looks massive, especially as it is exceedingly wide proximally* (Figs. 20, 22, 23). Distally it usually departs from the overlying uncus, leaving a wider gap than in *Poanes* (Figs. 20, 22, 23). In dorsal view tegumen plus uncus together suggest an elongate, caudally-tapering triangle. Distally the uncus splits into paired prongs which are medium long and close together (Fig. 19). (It is not "undivided" as claimed by Miller [1966:260].)

The saccus is short, as in *Poanes* (Figs. 20, 22, 23).



FIGS. 19–21. Male genitalia of *Paratrytone* sp. from Cuazimalpa [=Cuajimalpa, ca. 3000 m, 19°21′N, 99°18′W, Distrito Federal], MEXICO, July 1918, R. Mu[e]ller (X-2311) (USNM). Scale = 1.0 mm. **19,** Tegumen, uncus, gnathos, and top of vinculum in dorsal view; **20,** Complete genitalia (minus right valva) in left lateral view; **21,** Aedeagus in dorsal view. Note the two pairs of symmetric titillators, one dorsal and one ventral.



FIGS. 22, 23. Male genitalia of two species of *Paratrytone* ex Godman (1900: plate 93) and Skinner and Williams (1924b). The main problem with these figures, drawn from slide mounts in which *parts are not perfectly oriented,* involves the aedeagus whose *two pairs of symmetric titillators* do not adequately show. **22,** *Paratrytone rhexenor* from MEXICO; **23,** *Paratrytone snowi* from Morrison, Colorado, U.S.A.

Female Genitalia
(Figs. 24, 25)

The ductus bursae is short and broad (broader than in *Poanes*)—about the diameter of the corpus bursae where the two join. It runs forward (but not also upward and to the left as in *Poanes*). Lacking the intricate, sclerotized, lateral wrinkles-and-grooves of *Poanes,* it begins at the ostium bursae as a ring of sclerotization, broken dorsally into a pair of sclerotized bands.

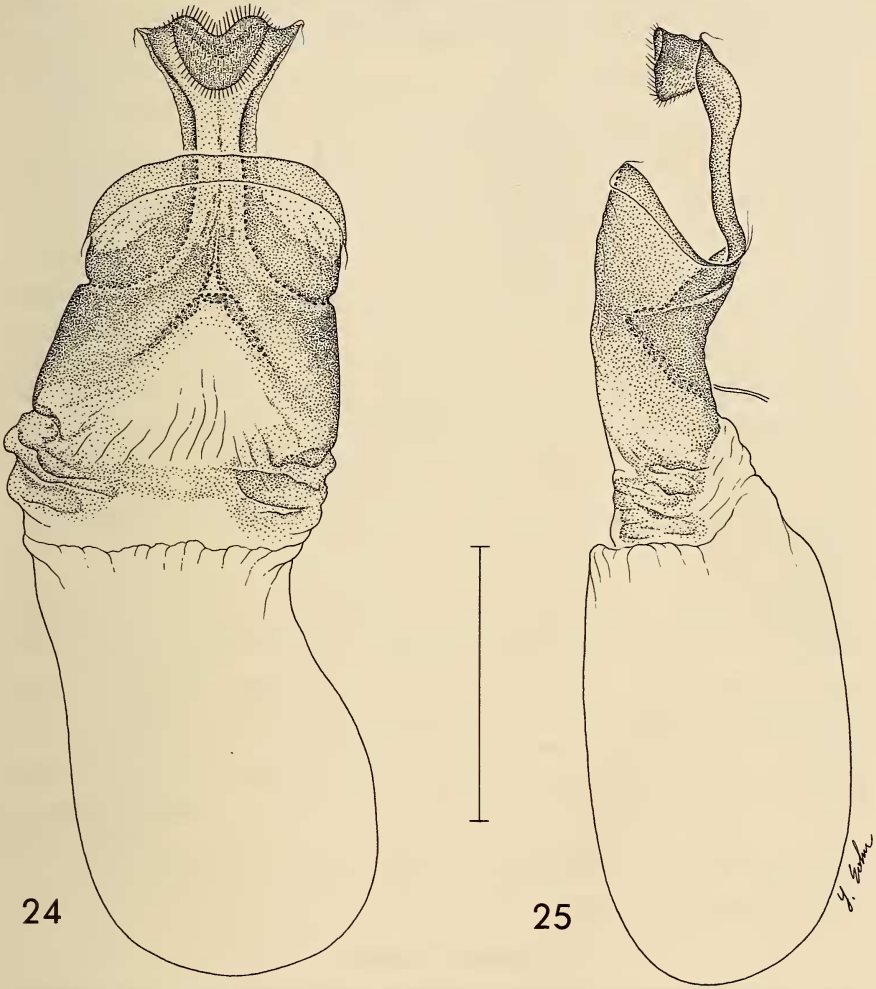
From the ostium bursae, these sclerotized bands initially converge and then diverge—like a pair of parentheses ") (" in reverse—as they extend backward the length of the laterally membranous lamella postvaginalis to attach to the upper, outer corners of a thick, heavily sclerotized, spinulose, transverse structure which (just in front of the ovipositor lobes) projects downward, and usually also forward, resembling, in ventral view, human lips.

Anterior to the dorsally broken sclerotized ring around the ostium bursae, the ductus bursae is always well sclerotized dorsally and sometimes variably sclerotized ventrally before becoming membranous. The dorsal sclerotized plate is invaginated middorsally in several species (including the one illustrated [*Paratrytone aphractoia*]). Ventrally, adjacent to the corpus bursae, is a more or less distinctive zone that varies from fully membranous to fully sclerotized. Viewed ventrally, this zone in several species suggests human female breasts or the brassiere that covers them (so that one is tempted to write *Paratytone*).

NOTES ON THE TERRESTRIAL SPECIES OF *POANES*

Poanes melane

I am returning *melane* (Edwards) to *Poanes*. Long ago when Dyar (1905) put only *melane, hobomok, zabulon,* and *taxiles* in *Atrytone,* the grouping was right but the genus, wrong, because none of those species is its type. Barnes and McDunnough's (1916:132) corrective step—"The species at present placed by Dyar in the genus *Atrytone* we would place, rather than create a new genus, in *Poanes* Scud. along with *massasoit,* with which they seem to possess considerable affinity"—



FIGS. 24, 25. Female genitalia of *Paratrytone aphractoia* from Mexico City, MEXICO, August 1920, R. Mu[e]ller (X-2307) (USNM). Scale = 1.0 mm. **24,** Sterigma and bursa copulatrix in ventral view; **25,** The same, plus part of the ductus seminalis, in right lateral view.

suited subsequent workers such as Lindsey (1921), Skinner and Williams (1924a), Comstock (1927), Lindsey et al. (1931), Bell (1938), and Hoffmann (1941). Skinner and Williams (1924a) went so far as to show the male genitalia of our four terrestrial species of *Poanes* (*hobomok, zabulon, taxiles,* and *melane*) in a single plate—reprinted in Lindsey et al. (1931) and now here (Figs. 8–11)—where both their distinctive form

and their close similarity leap out. All the same, when Evans (1955), without explanation, switched *melane* from *Poanes* to *Paratrytone*, everyone blindly followed him.

Putting the Californian *melane* back restores *Poanes* in the United States to transcontinental grandeur.

South of the border, *melane* extends to Panama in two superficially defined subspecies—the Mexican *vitellina* (Herrich-Schaeffer) and the Central American *poa* Evans—whose status vis-à-vis nominotypical *melane* warrants further study. Ten dissections of male genitalia indicate that both the lateral and the medial dorsally-pointing projections at the distal end of the valva are shorter and wider in the Californian *melane melane* (Fig. 11) than they are in the more southerly differentiates (Fig. 13), but also that they are longer and narrower in the geographically intermediate *melane vitellina* (dissections from the Mexican states of Veracruz, Puebla, Michoacán, Oaxaca, and Chiapas) than they are in the southernmost *melane poa* (dissections from Costa Rica and Panama)! The apparent polytypic species may be a superspecies.

All populations of *Poanes melane* exhibit a well-sclerotized, long and narrow cornutus comprising closely spaced, more or less longitudinal rows of numerous overlapping fine spines set in membrane whose curved shape suggests a cover for, say, the top and upper sides of a tiny caterpillar. It belongs to a more general class that I have dubbed "scouring-pad cornuti" (Burns unpubl.). Missing from most terrestrial species of *Poanes*, this cornutus is so conspicuous in *melane* that it appeared in the Godman (1900) and Skinner and Williams (1924a) figures of *melane* genitalia (Figs. 11, 13) and elicited a remark from Skinner and Williams (1924a:60): "The aedoeagus of *melane* . . . carries . . . a floating bundle of hair-like spines."

Poanes hobomok

Ranging from southern eastern and central Canada to the northern fringe of the southern eastern and central United States, *hobomok* is the most northern of the terrestrial species of *Poanes*. It seems to pose no genitalic problems. Apart from the tegumen/uncus looking more concave than usual in lateral view (imperfectly shown in Fig. 8), the male genitalia are fairly typical and without obvious idiosyncrasies.

Poanes hobomok is famous for having dimorphic females and for having catalyzed the symbol T_f for duration of copulation (Burns 1970). (The mean T_f of this skipper is 38¼ minutes.)

Poanes zabulon and *taxiles*

Claiming that their "abdominal structures [=genitalia] are the same," Scott (1986:452) made *taxiles* a subspecies of *zabulon*. For such a gen-

italically conservative group, *zabulon* and *taxiles* express what can only be considered major genitalic differences; and the two skippers are undoubtedly distinct species.

The biggest difference is also the easiest to see because it is at the distal end of the male genitalia on the outside of the valva. In *zabulon* a peculiar flap from the body of the valva extends backward, lateral to the lateral (dentate) dorsally-pointing projection, so as to hide it in lateral view (Fig. 26). This condition is unique among the terrestrial species of *Poanes*. In *taxiles* the body of the valva barely overlaps the dentate, dorsally-pointing projection (Fig. 27). And little (Figs. 2, 8, 16) to no (Figs. 5, 11, 13–15) overlap marks all the other species. The striking total overlap in *zabulon* does not show in previously published figures of its genitalia (Figs. 9, 12) because they give inside rather than outside views of the valva. I have verified this difference in many more males of *zabulon* and *taxiles*, from diverse localities, simply by examining the end of the genitalia *in situ*.

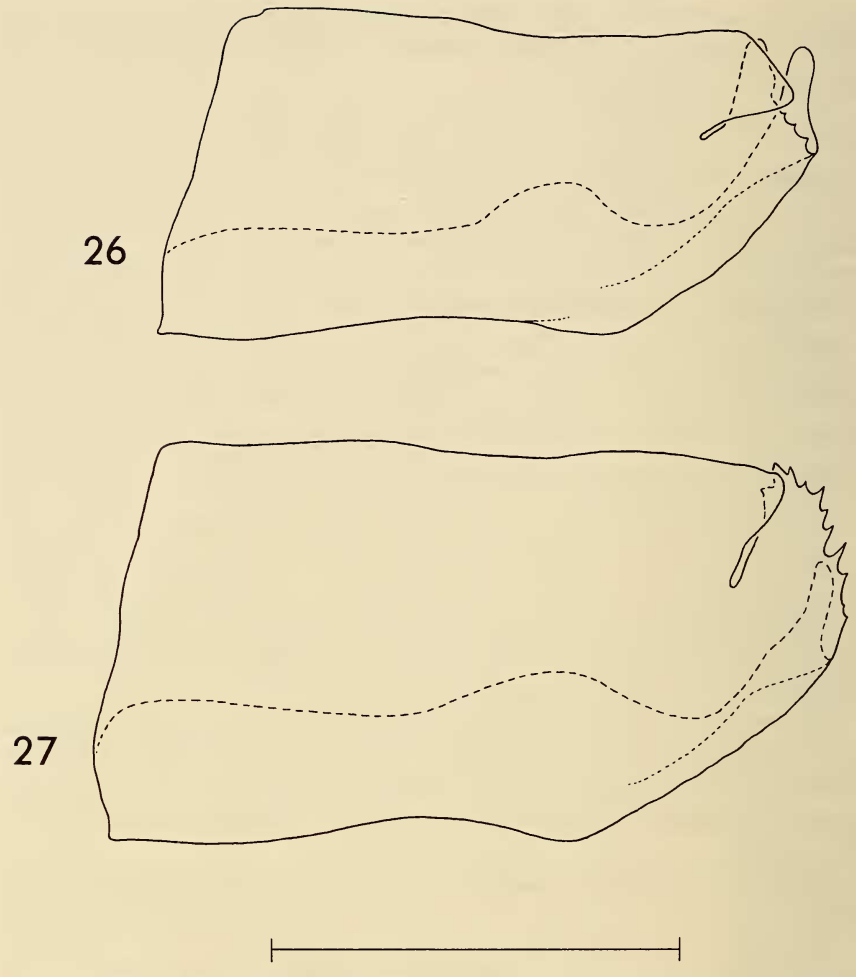
A large genitalic difference visible only in complete, KOH-treated dissections involves the posterior margin of the dorsal part of the anellus. Viewed dorsally, it looks in *zabulon* like a very shallow W (much shallower than the one in Fig. 3) but in *taxiles* like a relatively deep, broad U to incipient W (with the point of the W, if present, but slightly developed—not obvious the way it is in Fig. 7).

The medial dorsally-pointing projection at the distal end of the valva is rounded at its tip in both species but broader in *zabulon* than in *taxiles*. This difference, which is subtle, requires oblique views for proper detection; so it hardly shows in the strictly lateral views of Figs. 26 and 27.

Appropriately enough, Bailowitz and Brock (1991:9, 86) treated *taxiles* as a full species, observing that "Some [taxonomic] changes [of Scott 1986] (such as lumping *Poanes taxiles* as a subspecies of *P. zabulon*) go against our conservative grain and are mentioned but not followed." Despite my stress here on male genitalia, I will add in passing that these two species also differ from one another in aspects of the female genitalia, superficial appearance (amply illustrated in many sources), and size (*taxiles* is larger).

Poanes zabulon is strongly disjunct, ranging through most of the warmer eastern United States from southern New England, the bottom end of the Great Lakes, and southern Iowa to northern Florida and eastern Texas and, in mountains, from southern Mexico (Veracruz, Puebla, Jalisco, Michoacán, Guerrero, Oaxaca, Chiapas) to western Panama (Chiriqui). *Poanes taxiles* is montane from the central and southern Rocky Mountain region of the United States to northern (Durango, Sinaloa) and southern (Jalisco, Veracruz, Puebla) Mexico.

The taxon *psaumis* Godman (1900)—described from two females



FIGS. 26, 27. Left valva of the male genitalia of two species of *Poanes* in left lateral view. Scale = 1.0 mm. **26,** *Poanes zabulon* from Charleson Street, Annandale, Fairfax County, Virgina, U.S.A., 31 August 1979, J. M. Burns (X-3103) (USNM). **27,** *Poanes taxiles* from 0.8 km southeast of Clark Peak, Pinaleno Mountains, 2740 m, Graham County, Arizona, U.S.A., 26 June 1958, J. M. and S. N. Burns (X-3105) (USNM). Note how a caudally-projecting flap from the body of the valva hides the upper part of the dentate dorsally-pointing projection in *P. zabulon* but not in *P. taxiles*. This distal genitalic difference is easily revealed *in situ* by mere brushing of scales or, at most, a bit of dry dissecting.

from Jalisco, Mexico, as a species of *Phycanassa* Scudder (a synonym of *Poanes*) and currently treated as a subspecies of *taxiles*—is the same as *taxiles* (**new synonymy**).

Poanes azin and *macneilli*

In a two-line footnote to his original description of *psaumis*, Godman (1900:489) unintentionally described *azin*, "an allied form from Colombia . . . but . . . a very much smaller insect." Half a century later, Bell (1947) described this Colombian skipper again, this time as a subspecies, *richteri*, of *Poanes zabulon*. Ironically, I now find that there really is a second small orange-and-brown species of *Poanes* in Colombia. It and *azin* (=*richteri*) are sisters.

Bell (1947:7) wrote at the end of his description that "The male genitalia are the same as those of typical *zabulon*." Although wrong, this observation reemphasizes the basic genitalic similarity existing among terrestrial species of *Poanes*.

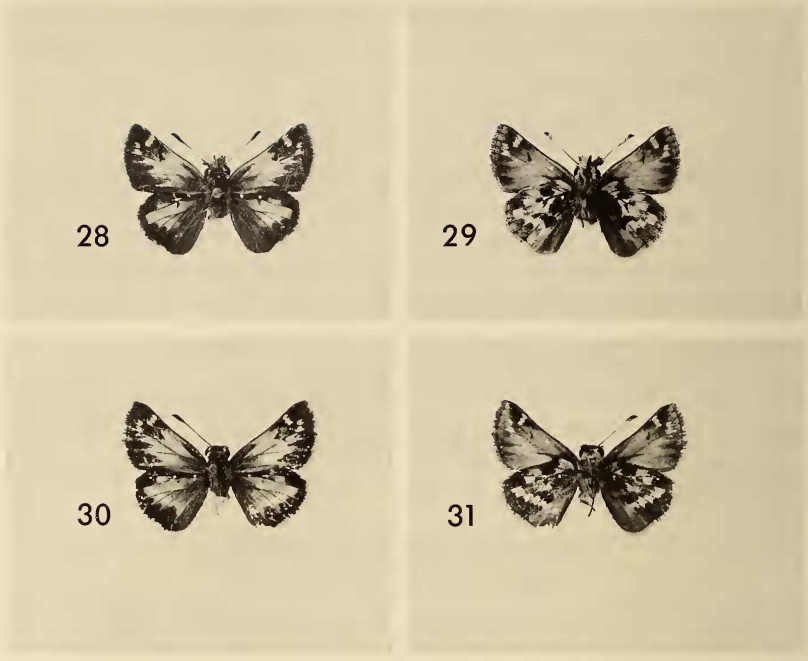
***Poanes macneilli*, new species**
(Figs. 1–3, 17, 18, 28–31)

Male genitalia. Paired uncus prongs short, in contact only at their tips (Fig. 1). Tegumen/uncus, in lateral view, moderately concave (Fig. 2)—more so than in *azin* (Fig. 5). Overlap between body of valva and lateral (dentate) dorsally-pointing projection small (Fig. 2)—but larger than in *azin*, where it is slight to nonexistent (Fig. 5). Medial dorsally-pointing projection at the distal end of the valva short (Fig. 2). Posterior margin of the dorsal part of the anellus decidedly W-shaped in dorsal view (Fig. 3)—more so than in any other terrestrial species of *Poanes* except *azin*, where the W is much deeper (Fig. 7). Aedeagus with a well-sclerotized, conspicuous scouring-pad cornutus (Fig. 3)—in this respect like *melane* but like no other terrestrial species of *Poanes*. (I have seen a vestigial scouring-pad cornutus in one male of *azin* and one male of *inimica*.)

Female genitalia. Caudally convex shelf that curves across the midline, just above and behind the ostium bursae, narrow, steeply arched, and evenly rounded across the middle (Fig. 17). Large, paired, rounded, internally spinulose pouches above, behind, and to the sides of the ostium bursae mostly membranous, but each with a narrowly triangular stripe of sclerotization tapering (toward the midventral line) across the middle of its dorsal wall (Fig. 17). (This sclerotized stripe continuous dorsally with the eighth tergite—Figs. 17, 18.) Well-sclerotized, spinulose to centrally bristled transverse element, just in front of the ovipositor lobes, wide and shallowly biconcave along its posterior margin in ventral view, with short central bristles (Fig. 17).

Size. Smaller than *azin* and therefore the smallest known species of *Poanes*: forewing length in males 12.6 and 13.2 mm, in female 13.6 mm. Comparative data for *azin*: with 6 males, 1 female at hand, Bell (1947) gave male forewing length as 14–16 mm, female, as 16 mm; with 31 males, 5 females, Evans (1955) reported a male forewing length of 15 mm; both my males measured 14.4 mm.

Facies. Upperside (Figs. 28, 30): A conspicuous vertical dark mark at the distal end of the forewing cell, narrower toward the costal margin and wider toward the inner margin. Large orange areas on both pairs of wings outwardly serrate—not as even as in *azin*. Row of orange subapical spots in spaces 6 to 8 of the forewing more nearly normal to the costal margin than in *azin*; orange spots in spaces 4 and 5 better developed than in *azin*. Orange spot in space 6 of the hindwing smaller than in *azin*.



FIGS. 28–31. *Poanes macneilli* from the Sierra Nevada de Santa Marta of COLOMBIA. (Even numbers, dorsal views; odd numbers, ventral views; all ×1.) **28, 29,** Holotype male; **30, 31,** Paratype female.

Underside (Figs. 29, 31): Much more boldly marked and contrasty than in *azin*, especially on the hindwing, where extremely dark spots (of dark brown overscaled with rust) occur, most notably in the middle of space 1b plus the bases of spaces 2 and 3, toward the base of space 7, and at the base of the wing. A pale median V-shaped band (composed of creamy yellowish spots in males, white spots in the female) runs from space 1c through spaces 2, 3, 4 and 5 (this is the apex of the V, after which is a slight break) to spaces 6 and 7. Pale overscaling (creamy or very light yellowish in males, lilac gray in the female) extends along the upper half of the outer margin of the forewing and along the outer margin of the hindwing as far as the yellow to dull orange abdominal fold.

Holotype. Male. COLOMBIA, Sierra Nev[ada] de S[an]ta Marta, E[ast] above San Pedro de la Sierra, 2900–3900 m, III-7-[19]75; M. J. Adams, Collector; GENITALIA NO. X-2352 J. M. Burns 1987. Deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Paratypes. Male. Same data as holotype, except genitalic dissection X-2364. Female. COLOMBIA, Sierra Nev[ada] de S[an]ta Marta, N[orth] of San Sebastian, 2800–3400 m, II-15-[19]75; M. J. Adams, Collector; GENITALIA NO. X-2365 J. M. Burns 1987. Both in the collection of C. D. MacNeill.

This new skipper comes from high on a very high (5775 m) and isolated continental "island" (next to the Caribbean Sea in northeastern Colombia), which is famous for its endemism (Adams 1973). True to its name, the Sierra Nevada de Santa Marta is permanently snow-

covered on top and, indeed, still glaciated. Sister species *azin* occurs well to the south, at similar elevations in the Colombian Andes, especially in the region of Tunja and Bogotá.

Poanes niveolimbus, monticola, capta and *ulphila* (**new combinations, all**)

This tight complex from montane southern Mexico and Guatemala is a mix of species and synonyms which have long been languishing in *Paratrytone*. The two species *Poanes niveolimbus* (Mabille) and *Poanes monticola* (Godman), although readily separable on the basis of a few stunning superficial features, have practically the same genitalia; I have found almost no consistent differences in a total of 14 male dissections. The modest differences apparent in the dorsally-pointing projections at the distal end of the valva in Godman's (1900) figures of these species (Figs. 14, 15) are individual rather than specific.

In males of this complex, the paired uncus prongs are long and delicate, with fine tips, and are in contact throughout their length (a set of states shared only with *melane*). The tegumen/uncus, in lateral view, is moderately concave (Figs. 14, 15) (about as in *macneilli*). There is little to no overlap between the body of the valva and the lateral (dentate) dorsally-pointing projection (Figs. 14, 15), but much variation in details of expression. The medial dorsally-pointing projection at the distal end of the valva is short (Figs. 14, 15). However, the posterior margin of the dorsal part of the anellus, in dorsal view, looks like an exceedingly flat W in *niveolimbus* but varies from slightly concave (unique among the terrestrial species of *Poanes*) through nearly straight to straight in *monticola*.

Poanes capta (Miller & Miller), described in *Paratrytone* in 1972 from three males and one female from montane Hidalgo, Mexico, is the same as *Poanes monticola* (**new synonymy**). Miller and Miller (1972) admitted that *capta* is very near *monticola* and *niveolimbus* but claimed that it differed from them in minor aspects of distal valval form and dorsal hindwing spotting. Both those characters vary enough that, in a good series of specimens, the supposed interspecific gaps vanish.

Since *capta* is really a *Poanes*, the following behavioral bit from Miller and Miller (1972:5) is of interest: "the few specimens [of *Paratrytone capta*] that were taken . . . did not seem as pugnacious as some *Paratrytone* we have encountered."

Judging from Plötz's four colored figures (copies in USNM), his *ulphila*, described from Mexico in 1883, is also in this complex; but, like specialists before me (Godman 1907, Hoffmann 1941, Evans 1955), I do not know the species. Possibilites run the gamut. At one extreme, with certain allowances for draftsmanship or for biological variation in

the model (neither was likely that wild!), at least two of Plötz's figures could be of *monticola*, in which case the older name *ulphila* would supplant it. At the other extreme, with so much convergence in color pattern among skippers, *ulphila* could be unrelated to the terrestrial species of *Poanes*.

Poanes monticola comes from high elevations in southern Mexico (Veracruz, Hidalgo, México, Distrito Federal, Puebla, Oaxaca); and *niveolimbus*, from high elevations in far southern Mexico (Chiapas) and Guatemala.

Poanes inimica and *lupulina*

On the basis of a very variable color character (the extent of a pale yellow area that begins near the tornus, in space 1b, on the underside of the forewing), Evans (1955) treated *lupulina* (Plötz) as a species distinct from *inimica* (Butler & Druce). I am returning *lupulina* to synonymy. According to geographic data in Evans, *lupulina* lies entirely within the range of *inimica*. Their genitalia strike me as identical.

Though *inimica* (Fig. 16) is plainly one of the boys (Figs. 1–16), its genitalia differ somewhat more (and more obviously) from those of the rest. The paired uncus prongs are long, but stouter than in any other species; and they are in contact only at their tips, which are blunt. The tegumen/uncus, in lateral view, is markedly concave (Fig. 16) (about as in *hobomok*). The medial dorsally-pointing projection at the distal end of the valva is long, but uniquely wide (about as wide as the lateral dorsally-pointing projection) and variously and irregularly truncate (Fig. 16). The posterior margin of the dorsal part of the anellus, in dorsal view, varies from nearly straight to an exceedingly flat W (not unusual). The right titillator is exceptionally long (Fig. 16).

Occurring at moderate elevations from Mexico (Tamaulipas, Veracruz, Hidalgo, Puebla, Morelos, Oaxaca, Chiapas) through Central America (Guatemala, Costa Rica, Panama) to northern South America (Colombia, Venezuela, Ecuador), *inimica* is the most southern of the terrestrial species of *Poanes*.

Fig. 32 conveys at a glance much of what I have done to straighten out the sorry polyphyletic mess in a couple of our heavily used and long stable skipper genera.

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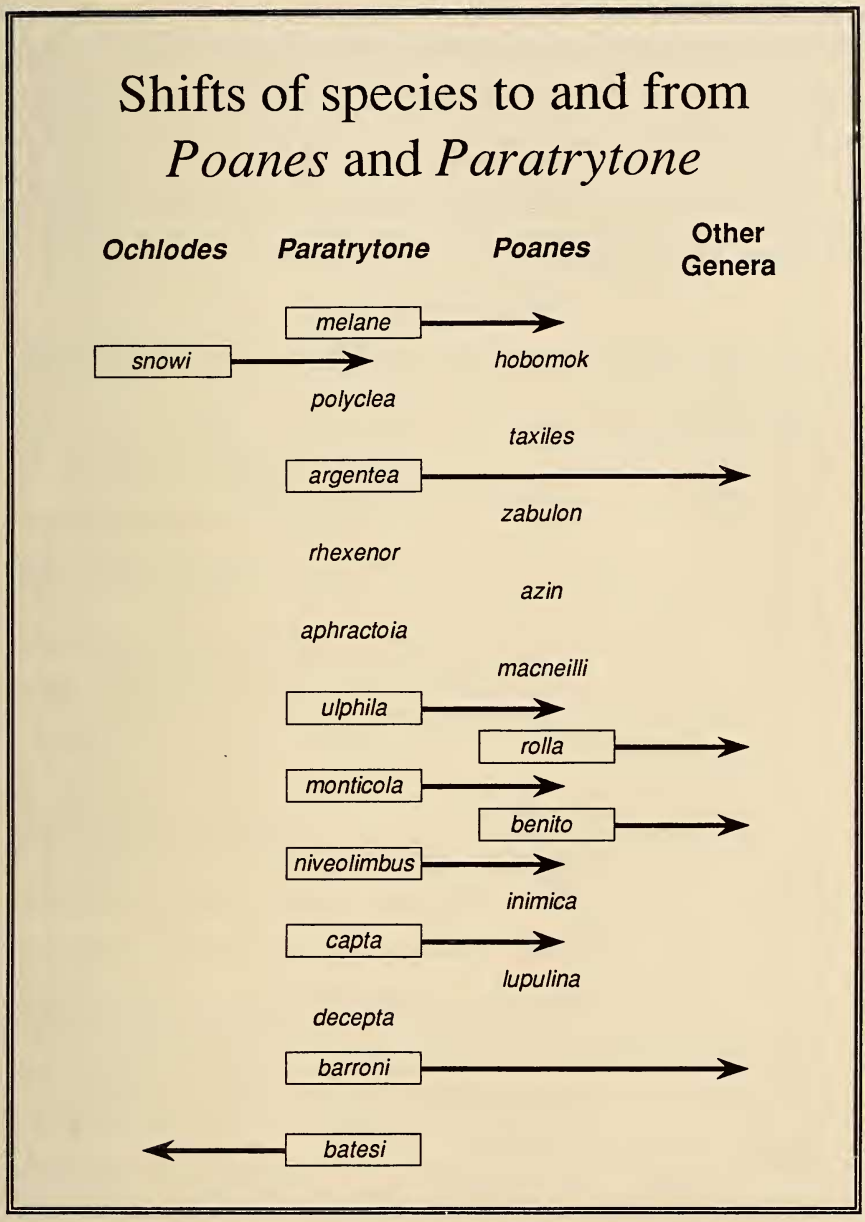

FIG. 32. Summary of species movements made in this paper.

at the American Museum of Natural History unequivocally referred the types of *azin* (Godman) and *zabulon richteri* Bell to the same photos (hence to one and the same species). Richard Robbins, Adrienne Venables, and Elizabeth Klafter dissected genitalia. Daniel Otte, Editor of the *Transactions of the American Entomological Society*, gave permission to reprint genitalic figures from Skinner and Williams (1924a, 1924b). Victor Krantz photographed those figures and others from Godman (1900), as well as the adults of *Poanes macneilli*. George Venable prepared Fig. 32. Young Sohn drew genitalic Figs. 1–7, 17–21, and 24–27 and mounted all figures. Don Harvey brought a couple of papers to my attention. Stan Shetler and the Research Opportunities Fund of the Smithsonian Institution supported relevant fieldwork in Arizona. At home, in the lab, and afield, Sarah Burns helped in ways too numerous or personal to mention.

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